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PHYTOPATHOLOGY

VOLUME IX NUMBER 2

FEBRUARY, 1919

THE PARASITISM OF PUCCINIA GRAMINIS TRITICI ERIKSS. AND HENN. AND PUCCINIA GRAMINIS TRITICI-COMPACTI STAK. AND PIEM.[1]

JULIAN G. LEACH[2]

WITH PLATES IV TO VI

Until recently only one biologic form of stem rust (*Puccinia graminis* Pers.) was known to occur on wheat. In 1916, however, Stakman and Piemeisel (20) collected a strain of stem rust on club wheat (*Triticum compactum*) and grasses in the Palouse district of Washington and Idaho which could not produce normal infection on a number of varieties of hard spring wheat which were very susceptible to a strain of *P. graminis tritici* collected at St. Paul, Minn. Although both strains attacked many varieties with equal vigor their action on these few hosts was distinctly different.

Although the two strains of rust were very similar morphologically, the size and shape of urediniospores differed appreciably (21). These physiological and morphological differences were sufficiently distinct to justify the designation of the new strain as a separate biologic form, *P. graminis tritici-compacti* Stak. and Piem.

A form apparently the same as that found in the Palouse district was later found to occur in the southern United States (22).

This discovery of the occurrence of more than one biologic form of stem rust on wheat seemed to have great economic importance as well as scientific interest. It appeared to explain to a large extent the diverse opinions as to the relative rust-resistance of various varieties of wheat in different sections of the country, for a variety resistant to stem rust in the Palouse

[1] Published with the approval of the Director as Paper No. 149 of the Journal Series of the Minnesota Agricultural Experiment Station.

[2] The writer is greatly indebted to Dr. E. C. Stakman, under whose direction the work was done, for assistance in defining the problem and for much helpful criticism throughout the work; and to Dr. R. A. Gortner, Chief of the Division of Agricultural Biochemistry, for many valuable suggestions.

district might be very susceptible if grown in the upper Mississippi valley; or, conversely, a variety susceptible in the upper Mississippi valley might be very resistant in the Palouse district. The importance of this in the problem of breeding wheat for resistance to stem rust was very evident. It was plain that a knowledge of the geographic distribution of these two forms and of the possible occurrence of other forms would be essential to efficient work in breeding for rust-resistance. Before these things could be determined it was necessary to know more about the infection capabilities of each of these two forms. It was also desirable to know whether they were constant and fixed or if they were mere variant strains that could be modified easily by host influences.

The objects of this work were, therefore:

1. To determine the comparative infection capabilities of *P. graminis tritici* and *P. graminis tritici-compacti* on various varieties of wheat.

2. To find more varieties, differing in degree of resistance to the two forms, which might be of value as differential hosts.

3. To determine further the degree of constancy and individuality of *P. graminis tritici-compacti.*

4. To investigate the basic factors underlying the action of the two forms in order to throw light on varietal resistance and biologic specialization.

MATERIALS AND METHODS

The work obviously involved the use of many varieties of wheat. These were obtained from several widely separated sections of the country, i.e., Minnesota, Kansas, Texas, Louisiana, Alabama and Washington.[3] The Minnesota varieties were pure line selections made in the Section of Plant Breeding, Division of Agronomy and Farm Management, University of Minnesota. Some of the remaining varieties also were pure line selections; others were not. Inoculation results indicated a relatively large percentage of mixed seed in several instances.

A strain of *P. graminis tritici-compacti* which was collected near Brundidge, Alabama, in May, 1917, and cultivated in the Plant Pathology greenhouse of the University of Minnesota since that date, was used throughout the experiments.

The strain of *P. graminis tritici* used was collected at University Farm, St. Paul, Minnesota, in the spring of 1916. Previous to its use in these experiments it had been cultivated on wheat for twenty-five generations.

[3] For supplying seed of the above varieties thanks are due to Prof. H. K. Hayes of the Minnesota Agricultural Experiment Station, Prof. L. E. Melchers, Kansas State Agricultural College, Mr. A. H. Leidigh, Texas Agricultural Experiment Station, Dr. C. W. Edgerton, Louisiana Agricultural Experiment Station and Mr. E. F. Gaines, State College, Washington.

The methods employed were essentially the same as those described by Stakman and Piemeisel (21).

Due to the close similarity of the two forms of rust used, every precaution was taken to prevent accidental infection. The two forms were kept in different sections of the greenhouse and, in so far as was practicable, only one form was worked with the same day. In fact, the majority of the inoculations with *P. graminis tritici-compacti* were completed before any work was done with the other form. The rusts were tested at frequent intervals by inoculating varieties of known resistance or susceptibility and at no time during the work was there any indication that contamination had occurred.

The strain of *P. graminis tritici-compacti* was grown on club wheat as a normal host and used for comparison throughout the work. Haynes Bluestem, Minn. 169, was used as the normal host for *P. graminis tritici.*

As a criterion for judging the relative resistance of a variety the character of infection was always used. Very little consideration was given to the number of uredinia because this is determined to a large extent by environmental conditions during the period of infection and is not necessarily an index to the resistance of the host. The number of uredinia may vary with the amount of inoculum, the relative percentage of viable spores used, and the moisture conditions during the first forty-eight hours after inoculation.

THE COMPARATIVE ACTION OF THE TWO BIOLOGIC FORMS ON VARIETIES OF WHEAT

The results of inoculating 72 varieties of wheat with the two biologic forms of rust are given in table 1. Each variety is listed under the name by which it was received. The state number is given wherever it is known and the varieties from each state are grouped together. The spring wheats are listed first, the hard winter wheats next, followed by the soft winter varieties. In the third column each variety is classified according to its relative "hardness." In making this classification the system described by Hayes, Bailey, Arny, and Olson (9) was followed. C., represents "corneous," S. C., "sub-corneous," S., "starchy," and S. S., "sub-starchy." The inoculation results are given in the form of a fraction, the denominator indicating the number of plants inoculated, and the numerator, the number which developed uredinia. The character of infection is always indicated.

The difference in infection capabilities of the two biologic forms was remarkably constant throughout all the tests. Of the 72 varieties inoculated, 52 showed various degrees of resistance to *P. graminis tritici-com-*

TABLE

Results of inoculations with Puccinia graminis tritici-compacti and Puccinia graminis tritici on varieties of wheat

NO.	VARIETY	TYPE	RELATIVE HARDNESS	SOURCE OF SEED	PUCCINIA GRAMINIS TRITICI-COMPACTI			PUCCINIA GRAMINIS TRITICI		
					Result	Number of trials	Character of infection	Result	Number of trials	Character of infection
1	Speltz Marz Minn. 337 NSN* I-00-45	Durum Spring	C.	Division of Agronomy and Farm Management, University of Minnesota	0/39	4	Numerous minute sharp dead areas	0/10	1	Heavily flecked
2	Mindum Minn. 470 NSN I-00-52	Durum Spring	C.	Division of Agronomy and Farm Management, University of Minnesota	1/20	2	Numerous minute sharp dead areas. One leaf with a few minute uredinia	0/10	1	Heavily flecked
3	Royalton Minn. 1037 NSN I-12-2	Common Spring	S. C.	Division of Agronomy and Farm Management, University of Minnesota	26/26	3	Small uredinia with well defined hypersensitive areas.	8/9	1	Heavy normal infection
4	Poultofka Minn. 1164 NSN I-13-3	Common Spring	S. C.	Division of Agronomy and Farm Management, University of Minnesota	17/18	2	Heavy normal infection	10/10	1	Heavy normal infection

* Nursery Series Number.

5	Bearded Bluestem Minn. 146 × Preston Minn. 168 NSN II-06-9	Common Spring	S. S.	Division of Agronomy and Farm Management, University of Minnesota	19/19	2	Small uredinia; little or no hypersensitiveness	9/9	1	Heavy normal infection
6	Marquis Minn. 1239 NSN I-15-177	Common Spring	S. C.	Division of Agronomy and Farm Management, University of Minnesota	3/28	3	Highly resistant; minute uredinia; sharp flecks and distinct dead areas	7/8		Heavy normal infection
7	Turkey Winter Minn. 578 × Fife Spring Minn. 165 NSN II-08-17	Common Spring	S. C.	Division of Agronomy and Farm Management, University of Minnesota	1/20	2	Highly resistant; minute uredinia; sharp flecks and distinct dead areas	10/10	1	Heavy normal infection
8	Turkey Winter Minn. 529 × Fife Spring Minn. 165 NSN II-08-21	Common Spring	S. S.	Division of Agronomy and Farm Management, University of Minnesota	5/20	2	Highly resistant; minute uredinia; sharp flecks and distinct dead areas	9/10	1	Heavy normal infection
9	Barletta Minn. 1178 C.I. 3297	Common Spring	S. S.	Division of Agronomy and Farm Management, University of Minnesota	21/152	15	Very highly resistant; extremely small uredinia; characteristic minute dead areas	45/47	5	Heavy normal infection

TABLE 1—*Continued*

No.	VARIETY	TYPE	RELATIVE HARDNESS	SOURCE OF SEED	PUCCINIA GRAMINIS TRITICI-COMPACTI			PUCCINIA GRAMINIS TRITICI		
					Result	Number of trials	Character of infection	Result	Number of trials	Character of infection
10	Turkey (Cosgrove) Minn. 529 NSN I-03-68	Common Winter	S. C.	Division of Agronomy and Farm Management, University of Minnesota	17/30	3	Uredinia small; distinctly hypersensitive	10/10	1	Heavy normal infection
11	Turkey Minn. 829	Common Winter	S. C.	Division of Agronomy and Farm Management, University of Minnesota	15/20	2	Uredinia medium in size; slightly subnormal	10/10	1	Heavy normal infection
12	Odessa Minn. 558 NSN I-01-3	Common Winter	S. S.	Division of Agronomy and Farm Management, University of Minnesota	19/19	2	Heavy normal infection	8/8	1	Heavy normal infection
13	Turkey Minn. 829 × Odessa Minn. 642 NSN II-02-280	Common Winter	S. C.	Division of Agronomy and Farm Management, University of Minnesota	18/19	2	Uredinia small; little or no hypersensitiveness	9/9	1	Heavy normal infection

14	Turkey Minn. 829 × Odessa Minn. 558 NSN II–02–14	Common Winter	S. C.	Division of Agronomy and Farm Management, University of Minnesota	15/20	2	Uredinia small with hypersensitive areas well defined	9/10	1	Heavy normal infection
15	Turkey Minn. 829 × Odessa Minn. 558 NSN II–02–195	Common Winter	S. C.	Division of Agronomy and Farm Management, University of Minnesota	29/29	3	Uredinia medium in size; slightly subnormal	9/9	1	Heavy normal infection
16	Odessa Minn. 642 × Turkey Minn. 829 NSN II–02–41	Common Winter	S. S.	Division of Agronomy and Farm Management, University of Minnesota	14/14	2	Small to medium uredinia; moderately hypersensitive	10/10	1	Heavy normal infection
17	Turkey Minn. 829 × Odessa Minn. 558 NSN II–02–190	Common Winter	S. C.	Division of Agronomy and Farm Management, University of Minnesota	17/19	2	Uredinia small with hypersensitive areas well defined	13/17	2	Heavy normal infection
18	Odessa Minn. 558 × Turkey Minn. 829 NSN II–02–81	Common Winter	C.	Division of Agronomy and Farm Management, University of Minnesota	18/20	2	Uredinia medium in size; slightly subnormal	7/8	1	Heavy normal infection

TABLE 1—*Continued*

NO.	VARIETY	TYPE	RELATIVE HARDNESS	SOURCE OF SEED	PUCCINIA GRAMINIS TRITICI-COMPACTI			PUCCINIA GRAMINIS TRITICI		
					Result	Number of trials	Character of infection	Result	Number of trials	Character of infection
19	Minn. 552 × Turkey Minn. 829 NSN II-02-521	Common Winter	C.	Division of Agronomy and Farm Management, University of Minnesota	17/18	2	Small uredinia with hypersensitive areas well defined	8/8	1	Heavy normal infection
20	S. P. I. 32766 NSN I-15-7	Common Winter	S.	Division of Agronomy and Farm Management, University of Minnesota	17/19	2	Heavy normal infection	6/9	1	Heavy normal infection
21	Harvest King Minn. 643 NSN I-15-26	Common Winter	S.	Division of Agronomy and Farm Management, University of Minnesota	20/20	2	Heavy normal infection	9/10	1	Heavy normal infection
22	Malakof Minn. 918 NSN I-15-155	Common Winter	S. C.	Division of Agronomy and Farm Management, University of Minnesota	19/21	2	Heavy normal infection	9/9	1	Heavy normal infection
23	Big Frame Minn. 1481 NSN I-06-6	Common Winter	S. C.	Division of Agronomy and Farm Management, University of Minnesota	17/19	2	Heavy normal infection	7/9	1	Heavy normal infection

24	Jones Longberry Minn. 1478 NSN I-06-6	Common Winter	S. C.	Division of Agronomy and Farm Management, University of Minnesota	17/19	2	Heavy normal infection	10/10	1	Heavy normal infection
25	Turkey (N. K. & Co.) Minn. 1488	Common Winter	S. C.	Division of Agronomy and Farm Management, University of Minnesota	19/21	2	Heavy normal infection	10/10	1	Heavy normal infection
26	Crimean Kan. P 765	Common Winter	S. C.	Kansas State Agricultural College	5/9	1	Extremely minute uredinia; other leaves heavily flecked	10/10	1	Heavy normal infection
27	Crimean Kan. 1627	Common Winter	C.	Kansas State Agricultural College	15/17	2	Variable; mostly small uredinia and hypersensitive. A few normal infections	10/10	1	Heavy normal infection
28	Kan. 373	Common Winter	S. C.	Kansas State Agricultural College	15/16	2	Variable; mostly small uredinia and hypersensitive. A few normal infections	9/9	1	Moderate infection, slightly subnormal. No definite hypersensitive areas

TABLE 1—*Continued*

No.	VARIETY	TYPE	RELATIVE HARDNESS	SOURCE OF SEED	PUCCINIA GRAMINIS TRITICI-COMPACTI			PUCCINIA GRAMINIS TRITICI		
					Result	Number of trials	Character of infection	Result	Number of trials	Character of infection
29	Kan. 2122	Common Winter	S. C.	Kansas State Agricultural College	18/20	2	Medium to minute uredinia; sharp hypersensitive areas. Variable	10/10	1	Good infection though slightly subnormal. No hypersensitive areas
30	Kan. 2123	Common Winter	S. C.	Kansas State Agricultural College	17/17	2	Variable; small uredinia with sharp hypersensitive areas to normal infection	8/9	1	Heavy normal infection
31	Alberta Red Kan. 2048	Common Winter	C.	Kansas State Agricultural College	15/17	2	Extremely minute uredinia; other leaves heavily flecked	10/10	1	Heavy normal infection
32	Alberta Red Kan. 2106	Common Winter	S. C.	Kansas State Agricultural College	19/19	2	Uredinia medium in size; sharp hypersensitive areas; variable.	10/10	1	Heavy normal infection
33	Red Winter Kan. 2132	Common Winter	S. S.	Kansas State Agricultural College	14/17	2	Variable; medium to minute uredinia with sharp hypersensitive areas	10/10	1	Good infection though slightly subnormal

34	Red Winter Kan 2101	Common Winter	S. C.	Kansas State Agricultural College	12/16	2	Variable; minute uredinia with hypersensitive areas to normal infection	11/12	1	Heavy normal infection
35	Red Winter Kan. 2102	Common Winter	S. C.	Kansas State Agricultural College	13/17	2	Variable; minute uredinia with hypersensitive areas to normal infection	10/10	1	Heavy normal infection
36	Red Winter Kan. 196	Common Winter	S. C.	Kansas State Agricultural College	4/9	1	Minute uredinia; other leaves heavily flecked. Sharp hypersensitive areas	9/9	1	Heavy normal infection
37	Turkey Kan. 2026	Common Winter	C.	Kansas State Agricultural College	7/17	2	Minute uredinia and large dead areas	9/10	1	Heavy normal infection
38	Turkey Kan. 570	Common Winter	S. C.	Kansas State Agricultural College	9/9	1	Minute uredinia and large dead areas	10/10	1	Heavy normal infection
39	Turkey Kan. 2098	Common Winter	C.	Kansas State Agricultural College	14/18	2	Variable; medium to minute uredinia with sharp hypersensitive areas	7/8	1	Moderate infection, slightly subnormal

TABLE 1—*Continued*

NO.	VARIETY	TYPE	RELATIVE HARDNESS	SOURCE OF SEED	PUCCINIA GRAMINIS TRITICI-COMPACTI			PUCCINIA GRAMINIS TRITICI		
					Result	Number of trials	Character of infection.	Result	Number of trials	Character of infection
40	Turkey Kan. 2029	Common Winter	S. C.	Kansas State Agricultural College	9/10	1	Variable; normal infection to minute uredinia with sharp hypersensitive areas	10/10	1	Good infection, slightly subnormal
41	Turkey Kan. 2039	Common Winter	S. C.	Kansas State Agricultural College	11/15	2	Minute uredinia; distinct hypersensitive areas	7/8	1	Heavy normal infection
42	Turkey Kan. P. 1082	Common Winter	S. C.	Kansas State Agricultural College	19/19	2	Variable; minute uredinia with distinct hypersensitive areas to normal infection	9/10	1	Heavy normal infection
43	Beloglina Kan. P. 750	Common Winter	S. C.	Kansas State Agricultural College	9/18	2	Minute uredinia; distinct hypersensitive areas	10/10	1	Heavy normal infection
44	Bearded Fife Kan. 2094	Common Winter	S. C.	Kansas State Agricultural College	25/37	4	Minute uredinia; distinct hypersensitive areas	8/9	1	Good infection, slightly subnormal. No hypersensitiveness
45	Champanka Kan. 1183	Common Winter	S. C.	Kansas State Agricultural College	17/18	2	Variable; uredinia medium in size; distinctly hypersensitive	10/10	1	Heavy normal infection

46	Kharkoff Kan. 2001	Common Winter	S. C.	Kansas State Agricultural College	14/17	2	Small uredinia; distinctly hypersensitive. Variable	7/9	1	Heavy normal infection
47	Kanred P 762 Kan. 2401	Common Winter	S. C.	Kansas State Agricultural College	17/18	2	Minute to medium uredinia; distinct hypersensitive areas	0/10	1	Dead areas at tips of leaves
48	P 1066 Kan. 2415	Common Winter	S. C.	Kansas State Agricultural College	18/30	3	Minute to medium uredinia; distinct hypersensitive areas	0/10	1	Dead areas at tips of leaves
49	P 1068 Kan. 2414	Common Winter	S. C.	Kansas State Agricultural College	18/37	4	Minute to medium uredinia; distinct hypersensitive areas	0/10	1	Dead areas at tips of leaves
50	Romanella Kansas P 1036	Common Winter	C.	Kansas State Agricultural College	15/17	2	Variable; normal infection to minute uredinia with sharp hypersensitive areas	10/10	1	Heavy normal infection
51	Iowa Red Winter Kansas P 706	Common Winter	S. C.	Kansas State Agricultural College	17/18	2	Variable. Good infection; uredinia medium in size; slightly hypersensitive	10/10	1	Heavy normal infection
52	Pesterboden Kan. 1635	Common Winter	S. C.	Kansas State Agricultural College	11/17	2	Variable; normal infection to minute uredinia; sharp hypersensitive areas; numerous flecks	8/10	1	Heavy normal infection
53	Hungarian Kan. 2194	Common Winter	S. C.	Kansas State Agricultural College	7/9	1	Good infection; slightly subnormal	10/10	1	Heavy normal infection

TABLE 1—*Continued*

No.	VARIETY	TYPE	RELATIVE HARDNESS	SOURCE OF SEED	PUCCINIA GRAMINIS TRITICI-COMPACTI			PUCCINIA GRAMINIS TRITICI		
					Result	Number of trials	Character of infection	Result	Number of trials	Character of infection
54	Kansas P 2141	Common Winter	C.	Kansas State Agricultural College	11/14	2	Minute uredinia; distinct hypersensitive areas	10/10	1	Heavy normal infection
55	Kan. (Is) 1644	Common Winter	C.	Kansas State Agricultural College	14/18	2	Minute uredinia; distinct hypersensitive areas	10/10	1	Heavy normal infection
56	Kharkof T.S. 1500	Common Winter	S. C.	Texas Substation No. 6, Denton, Texas	21/27	3	Small uredinia; distinctly hypersensitive	10/10	1	Heavy normal infection
57	Kharkof T.S. 583	Common Winter	S. S.	Texas Substation No. 6, Denton, Texas	26/30	3	Small uredinia; distinctly hypersensitive	10/10	1	Heavy normal infection
58	Turkey T.S. 1497	Common Winter	S. S.	Texas Substation No. 6, Denton, Texas	7/17	2	Variable; very hypersensitive to normal infection	9/10	1	Medium to large uredinia; slightly subnormal
59	Crimean T.S. 1499	Common Winter	S. C.	Texas Substation No. 6, Denton, Texas	27/31	3	Minute to medium uredinia; distinctly hypersensitive	3/50	5	Normal infection on three plants. Other plants developed no uredinia; no flecks

60	Bartgrosskörniger T.S. 1504	Common Winter	S.	Texas Substation No. 6, Denton, Texas	16/16	2	Heavy normal infection	10/10	1	Heavy normal infection
61	Ferguson's Mediterranean	Common Winter	S.	Texas Substation No. 6, Denton, Texas	18/24	3	Variable; very hypersensitive to normal infection	9/10	1	Heavy normal infection
62	Mediterranean	Common Winter	S.	Texas Substation No. 6, Denton, Texas	30/30	3	Good infection, slightly subnormal	9/9	1	Heavy normal infection
63	T.S. 709	Common Winter	S.	Texas Substation No. 5, Temple, Texas	15/17	2	Heavy normal infection	10/10	1	Heavy normal infection
64	Forester's Bluestem Mediterranean	Common Winter	S.	Texas Substation No. 5, Temple, Texas	16/19	2	Small uredinia; distinctly hypersensitive	10/10	1	Heavy normal infection
65	Farmer's Mediterranean	Common Winter	S.	Texas Substation No. 5, Temple, Texas	23/29	3	Small uredinia; distinctly hypersensitive	10/10	1	Heavy normal infection
66	T.S. 2399	Common Winter	S.	Texas Substation No. 5, Temple, Texas	9/10	1	Heavy normal infection	7/9	1	Heavy normal infection
67	Red May	Common Winter	S.	Louisiana Agricultural Experiment Station, Baton Rouge, La.	10/10	1	Heavy normal infection	10/10	1	Heavy normal infection

TABLE 1—*Concluded*

No.	VARIETY	TYPE	RELATIVE HARDNESS	SOURCE OF SEED	PUCCINIA GRAMINIS TRITICI-COMPACTI			PUCCINIA GRAMINIS TRITICI		
					Result	Number of trials	Character of infection	Result	Number of trials	Character of infection
68	Fulcaster	Common Winter	S.	Louisiana Agricultural Experiment Station, Baton Rouge, La.	10/10	1	Heavy normal infection	10/10	1	Heavy normal infection
69	Purple Straw	Common Winter	S.	Louisiana Agricultural Experiment Station, Baton Rouge, La.	18/20	2	Heavy normal infection	8/9	1	Heavy normal infection
70	Golden	Common Winter	S.	Louisiana Agricultural Experiment Station, Baton Rouge, La.	9/10	1	Heavy normal infection	9/9	1	Heavy normal infection
71	Alabama Bluestem	Common Winter	S.	Alabama Agricultural Experiment Station, Auburn, Ala.	20/20	2	Heavy normal infection	10/10	1	Heavy normal infection
72	Coppei	Club Spring	S. S.	Washington Agricultural Experiment Station, Pullman, Wash.	20/20	2	Heavy normal infection	20/20	2	Heavy normal infection

pacti, while only 13 varieties gave indication of resistance to *P. graminis tritici*. Inconsistencies occurred on only a few varieties and these undoubtedly could be attributed to mixed seed. It will be noted that those varieties which are resistant to *P. graminis tritici* are also resistant to *P. graminis tritici-compacti* but not always to the same degree. Several varieties, however, which are highly resistant to *P. graminis tritici-compacti* are completely susceptible to *P. graminis tritici* (plates IV and VI). In all cases, those varieties which show normal susceptibility to *P. graminis tritici-compacti* are also very susceptible to *P. graminis tritici*.

Among the varieties tested all degrees of susceptibility and resistance were found, ranging from heavy normal infection to almost complete immunity. Of the spring wheats, Mindum, Speltz Marz, Royalton, Marquis, and Barletta showed a high degree of resistance to *P. graminis tritici-compacti* (plates IV, V and VI). The Turkey Winter × Fife Spring Hybrids were also very resistant while the Bluestem × Preston hybrid was only semi-resistant. Poultofka, a soft spring wheat, was very susceptible. All of these spring varieties were highly susceptible to *P. graminis tritici* with the exception of the two durum varieties, Mindum and Speltz Marz. These two varieties were equally resistant to both forms of rust.

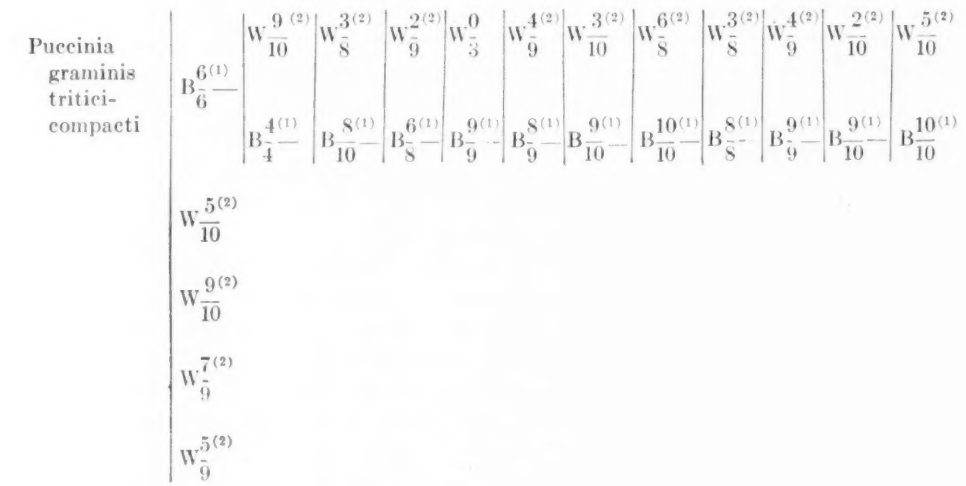
The lesions produced on resistant varieties were characteristic for each variety and for each form of rust and were consistently the same in each successive trial. On Barletta, when inoculated with *P. graminis tritici-compacti*, only a few extremely small uredinia, surrounded by a small area of dead tissue, were formed. Many minute areas of leaf tissue were killed without the formation of uredinia. On Royalton the uredinia were larger and were surrounded by a more extensive area of either dead or almost dead tissue. The lesions on Marquis were very similar to those on Royalton although there seemed to be a greater tendency of the hypersensitive areas to coalesce. Large normal uredinia were produced on all three of these varieties when inoculated with *P. graminis tritici*.

The hard winter varieties showed varying degrees of resistance to *P. graminis tritici-compacti*. The majority of them, however, were very resistant, especially those of the Turkey or Crimean group. Only a few varieties showed any resistance to *P. graminis tritici*, three of which were, however, highly resistant. These were the varieties, Kanred P 762 (Kan. 2401), P 1066 (Kan. 2415) and P 1068 (Kan. 2414), developed at the Kansas Experiment Station and reported as resistant to "stem rust" (14). They developed no uredinia when inoculated with *P. graminis tritici* but were only semi-resistant to *P. graminis tritici-compacti*. Recently these varieties have been shown to be susceptible also to certain other biologic forms of stem rust (11, 15).

Nearly all of the soft winter wheats from Texas, Louisiana and Alabama, were susceptible to both forms of rust. The varieties of Mediterranean wheat from Texas were moderately resistant to *P. graminis tritici-compacti*. The variety listed, as T.S. 1499 which was highly resistant to *P. graminis tritici* and semi-resistant to *P. graminis tritici-compacti* was found upon inquiry to be the same as the Kansas variety Kanred, P 762, having been introduced into Texas in 1914.

By referring to table 1 it can be seen that a classification of the varieties according to geographic source classifies them also with remarkable accuracy in regard to susceptibility and resistance to *P. graminis tritici-compacti*. There is also a decided correlation between the hardness and softness of wheat varieties and their resistance or susceptibility to this form. There are, however, a few exceptions. Again, the spring wheats as a class are more resistant to *P. graminis tritici-compacti* than the winter wheats. In general it can be said that, with a few exceptions, the hard spring wheats are resistant to *P. graminis tritici-compacti* while the soft winter wheats are susceptible (plate V). Nothing can be said as to the true significance of this fact, although it is very probable that the same factor which determines these characters also determines the resistance or sus-

DIAGRAM 1. RESULT OF BRIDGING EXPERIMENT WITH PUCCINIA GRAMINIS TRITICI-COMPACTI



B—Barley, Manchuria, Minn. 105
W—Wheat, Haynes Bluestem Minn. 169
CW—Club wheat, Brown Gloria
(1) Normal infection for this host.
(2) Extremely hypersensitive, minute uredinia and numerous flecks.

ceptibility of the variety to *P. graminis tritici-compacti*. Whatever may be learned about the geographic distribution of biologic forms it is very likely that the relative abundance of *P. graminis tritici-compacti* in a given region will be determined largely by the type of wheats grown.

THE CONSTANCY OF THE TWO BIOLOGIC FORMS

Although it appears to have been proven conclusively that biologic forms of *P. graminis* cannot be changed to any great extent by the use of bridging hosts or other methods (23, 24), on account of the very slight differences between these two forms it was thought advisable to make further effort to break down these differences by means of host influences. There are two methods by which, theoretically, this change could be

DIAGRAM 2. RESULTS OF SUCCESSIVE TRANSFERS OF PUCCINIA GRAMINIS TRITICI-COMPACTI TO RESISTANT HOSTS

Puccinia graminis tritici-compacti

CW— $\mathrm{CW}\frac{10^{(3)}}{10}\mathrm{CW}\frac{10^{(3)}}{10}\mathrm{CW}\frac{10^{(3)}}{11}\mathrm{CW}\frac{10^{(3)}}{10}\mathrm{CW}\frac{9^{(3)}}{10}\mathrm{W}\frac{6^{(1)}*}{10}$

$\mathrm{W}\frac{8^{(1)}}{10}\mathrm{W}\frac{3^{(1)}}{10}\mathrm{W}\frac{0}{4}**$

$\mathrm{BF}\frac{8^{(4)}}{10}\mathrm{Ro}\frac{1^{(5)}}{8}\mathrm{W}\frac{0}{2}$

$\mathrm{Bar}\frac{2^{(6)}}{10}\mathrm{Bar}\frac{0}{8}$

Od— $\mathrm{AR}\frac{10^{(4)}}{10}\mathrm{Ro}\frac{8^{(1)}}{9}\mathrm{W}\frac{1^{(1)}}{3}\mathrm{W}\frac{0}{1}$

W = Haynes Bluestem, Minn. 169
BF = Bearded Fife, Kan. 2094
Od = Odessa, Minn. 558
AR = Alberta Red, Kan. 2106
Ro = Royalton, Minn. 1037
Bar = Barletta, Minn. 1178
CW = Club wheat, "Brown Gloria"
(1) Extremely hypersensitive; minute uredinia and numerous flecks.
(2) Medium to minute uredinia; sharp hypersensitive areas.
(3) Heavy, normal infection.
(4) Medium uredinia; sharp hypersensitive areas.
(5) Extremely minute uredinia; numerous small sharp dead areas.
(6) Extremely minute uredinia; numerous small sharp dead areas; one leaf with several fairly large uredinia.
* Control culture.
** This experiment was repeated several times with the same results.

brought about; (a) the use of "bridging hosts" and (b) by the constant association of the rust with an uncongenial host.

To test the first of these methods *P. graminis tritici-compacti* was grown for a number of consecutive generations on barley, which is a common host for the two forms. From each generation on barley, transfers were made to Haynes Bluestem (Minn. 169) which is resistant to *P. graminis tritici-compacti*. Diagram 1 shows the results of this experiment. After growing for eleven generations on barley, the rust did not infect Haynes Bluestem any more vigorously than it had at the beginning of the experiment.

To determine the effect of constant association of the rust with an uncongenial host attempts were made to propagate *P. graminis tritici-compacti* continually on a single resistant variety or successively on several resistant varieties.

Diagram 2 gives the results of these attempts. In all cases the rust, instead of increasing in vigor, appeared to become weaker; and for this reason, together with the decreasing amount of inoculum, ran out entirely after a few generations.

These results furnish additional evidence that the two biologic forms are constant and well fixed.

RUST-RESISTANCE AND BIOLOGIC SPECIALIZATION

The biologic specialization as shown by these two forms is of added interest in that it gives us a new viewpoint on the possible basis of rust-resistance.

Much work has been done in the past with the view of discovering the fundamental causes of rust-resistance. Many varied explanations have been offered. Since the literature on this subject has been thoroughly reviewed by Stakman (18) only the most important works will be mentioned here.

Anderson (1) states that the flinty, hard varieties of wheat are more resistant to rust due to their high silica content.

Comes (5), working with wheat rust, concluded from observation and analysis that the biochemical factor which enables plants to resist parasitic fungi is the acidity of the cell sap.

Cobb (3) attempted to explain resistance of wheat to rust as due entirely to morphological characters of the host, such as small stomata, thick epidermis, waxy coating, etc.

Ward (26), however, working with the brown rust of bromes, proved conclusively that resistance was independent of any morphological characters of the host.

Stakman (18) has shown that when a resistant host is inoculated with certain biologic forms of *Puccinia graminis* a limited number of cells near the point of infection are killed and the fungus fails to develop normally. In normal infection of a susceptible host, however, the fungus grows vigorously without serious injury to the host cells. This injury of the cells of a resistant host was termed hypersensitiveness. The degree of hypersensitiveness was observed to vary in direct proportion to the degree of resistance of the host.

Freeman (7, p. 115) calls attention to the difference between disease escaping, disease enduring, disease resisting and immune varieties, and states that, "The exact nature of the cytologic forces which make possible or impossible a parasitic reaction are only partially understood. . . . The possible rôle of enzymes in such inter-reactions is suggestive and recent activity in the study of enzymes from the standpoint of the biologist and chemist bids fair to throw much needed light on cell activities."

The work of Marshall Ward, who first carefully investigated the intimate relations between host and rust parasite, is of outstanding importance and is worthy of careful review.

After proving that the morphological characters of the host had no influence upon true resistance, Ward (25) began a careful histological study of the phenomena involved in the infection of resistant bromes by *Puccinia dispersa*. He showed that the germ tube gained entrance through the stomata in a normal manner, but instead of developing normally it either killed a few cells and then disintegrated, or grew very slowly and never produced pustules. In normal infection he pointed out that no immediate injury to the host cells was noticeable and that a fine adjustment between host and parasite, resembling a state of symbiosis, was the result. A wide range in degree of resistance was found and he noted that the resistance varied inversely with the ability of the fungus to enter into this symbiotic relation with the host cells. He (27, p. 151) explains this action as follows: "All evidence points to the existence in the cells of the fungus of enzymes or toxins, or both, and in the cells of the host plant anti-toxins or similar substances, as a decisive factor in infection or immunity, although I have as yet failed to isolate any such bodies."

Ward's histological work has been verified by Marryat with *Puccinia glumarum* and semi-immune host plants, by Gibson with *Uredo chrysanthemi* and many hosts widely separated taxonomically, and by Stakman (18, 19) with several biologic forms of *Puccinia graminis* and hosts both partially and highly resistant. In the latter work attention is called to the fact that, "The relations between plant and parasite in partially resistant and almost immune plants are different in degree only."

In further work on the problem, Ward (36, p. 272), in attempting to detect the presence of toxins or anti-toxins, germinated urediniospores in leaf extracts of congenial and uncongenial hosts. Concerning this experiment he states, "All attempts of this kind were in vain, however, since vigorous spores germinate equally well in extracts of the leaves of their own host-species and of their antagonistic host-species. . . . The positive results do show, however, that the failure of spores from *B. mollis* to develop pustules on *B. sterilis*, for instance, is not due to mere exudation of some antagonistic soluble extract,—the antagonism must be due to something far more subtle than a mere soluble poison oozing from the cells."

This work has been verified by the writer, but since it is possible that toxins or anti-toxins may be formed as a direct result of fungus invasion as suggested by Bolley (2) it was thought advisable to make an effort to detect the presence of such substances in the immediate region of rust infection. Accordingly the following experiment was carried out.

Three varieties of wheat showing varying degrees of resistance were selected, viz., (a) Barletta (Minn. 1178), highly resistant to *P. graminis tritici-compacti*, (b) Haynes Bluestem (Minn. 169), semi-resistant to *P. graminis tritici-compacti*, (c) Brown Gloria (club wheat), very susceptible to *P. graminis tritici-compacti*. All three varieties are very susceptible to *P. graminis tritici*. Ten plants of each of the above hosts were inoculated with the two forms of rust. Ten plants of each variety were left uninoculated as checks. After twelve days the plants inoculated with *P. graminis tritici* were all developing large, normal uredinia, but of those inoculated with *P. graminis tritici-compacti* only the club wheat was showing normal infection. On the Haynes Bluestem (Minn. 169) there were a few minute uredinia and numerous distinct flecks, while on Barletta there was no indication of the development of uredinia, merely a few extremely minute dead areas.

Late in the afternoon of the twelfth day after inoculation, these infected areas and also an equal area of the uninfected plants were carefully trimmed out, put in separate test tubes, placed out over night and allowed to freeze. The temperature was well below zero (Fahrenheit). Early the following morning each sample was thoroughly ground in a mortar with the addition of 1 cc. of distilled water. This liquid extract was then filtered under pressure and from each sample hanging-drop sowings were made with urediniospores of each of the two rusts. These sowings were made in duplicate and check sowings of each rust were made in distilled water.

The germination of the spores was watched at frequent intervals for twenty-four hours after sowing and notes taken on each set. Germination was complete in the entire series after about seven hours. After this time the germ tubes ceased to grow, became vacuolated, somewhat twisted and

a few showed signs of disintegration. This deterioration of the germ tubes was general for all members of the series and no appreciable differences in this respect could be detected between the individual sowings. The notes were tabulated and a study of the table showed that, although there was considerable variation in the percentage of germination and in length of germ tubes, there was no correlation with the resistance of the host from which the extract was made. This experiment gives no evidence that there is a toxic substance secreted by a resistant host in response to rust infection.

Ward, being unable to demonstrate the presence of toxins and antitoxins in resistant hosts to uphold his hypothesis, continued his investigations further, approaching the question from a slightly different viewpoint. He performed numerous experiments to test the effect of mineral starvation on resistance and susceptibility. From these experiments he concluded (27, p. 145) that, "Lack of minerals in no way secured immunity from infection though seedlings deficient in phosphorus or in nitrogen tended to show retardation of infection." Failing to find any satisfactory evidence in this work, he again fell back upon his toxin and anti-toxin hypothesis.

Similar results on the effect of mineral elements on susceptibility and resistance to *P. graminis* have also been reported by Stakman (18).

Finally Ward (28, p. 38), in his last published work on this problem, describes the development of hyphae of *P. glumarum* in a resistant wheat as follows: "In short these hyphae show evident signs of degeneration in all respects, and we conclude, from comparison with experimentally starved hyphae, that they are undergoing death-changes owing to one of two events viz., they are either starving from the want of food supplies or they are being poisoned."

Concerning the nature of the "experimentally starved hyphae," which were obtained by keeping previously infected leaves in a carbon dioxide-free atmosphere, he remarks (28, p. 41): "The phenomena—starvation of hyphae in a nest of dead cells, or the corrosion of cells beneath the spores sown on a leaf—*are similar in all cases to what occurs on the so-called immune plants we have dealt with.*"

This comparison, however significant it may have appeared to Ward, was not sufficient to cause him to discard his previous hyphothesis which he restates in this paper (28, p. 21) as follows: "In other words, infection, and resistance to infection, depend on the power of the fungus-protoplasm to overcome the resistance of the cells of the host by means of enzymes or toxins; and reciprocally, on that of the protoplasm of the cells of the host to form anti-bodies which destroy such enzymes or toxins, or to excrete chemotactic substances which repel or attract the fungus-protoplasm."

In the light of our present knowledge of biologic specialization and of observations made during the course of this work, this hypothesis is very unsatisfactory.

It is unsatisfactory, first, because no one has yet been able to demonstrate the existence of either toxins or anti-toxins in the host plant cells or in the fungus. Ward admitted that he was unable to detect any such substance in the leaf extract of resistant hosts and the writer has verified this and has also been unable to detect any substance toxic to germinating spores in extracts from leaves of uncongenial hosts, the material being taken in the immediate region of infection.

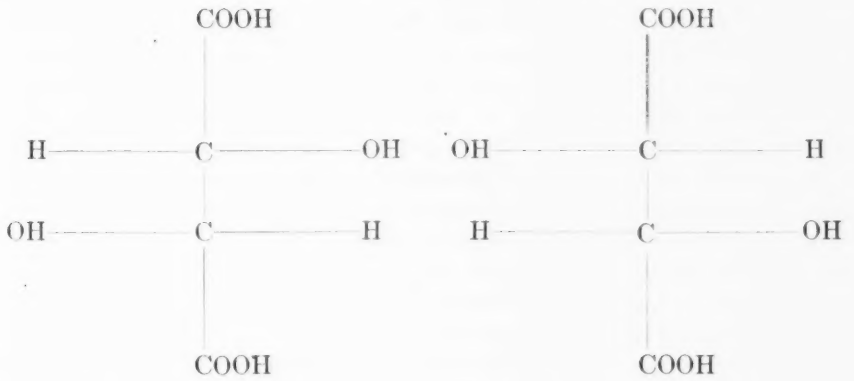
In the second place, these toxins or anti-toxins, if they should exist, would necessarily have to be specific for each form of rust, else we could not account for such phenomena as we find with the biologic forms described in this paper where a given host is highly resistant to one form and very susceptible to another.

Moreover, since it has been shown that the phenomenon of resistance is the same in hosts partially resistant and in those highly resistant (13, 19) we must assume that these toxins or anti-toxins are present in all plants, even those widely separated taxonomically from the type host of the rust. We would have to assume that all plants possess this peculiar substance except those few species which are susceptible to the rust.

Our inability to account for specific toxins in all these cases and our present knowledge of biologic specialization in rusts, together with facts observed in the present work, strongly indicate that rust-resistance may not be a phenomenon involving toxins and anti-toxins. On the contrary, viewed in the light of recent researches in stereochemistry and enzyme activity, it seems reasonable to suppose that it may be rather one of specific food relations, i.e., a specificity of food requirements on the part of the fungus and a specificity of food production on the part of the host.

This hypothesis involves two assumptions; first, that each biologic form of rust has a specific food requirement and, second, that the products of cell metabolism are specific for each species and variety of host plant.

As evidence in behalf of the first assumption several examples of known specificity of food requirements among fungi may be mentioned. The classical example of the specificity of the action of *Penicillium glaucum* in relation to dextro-, levo-, and racemic-tartaric acids first demonstrated by Pasteur in 1861 is well known. Dextro- and levo-tartaric acids differ only slightly in molecular configuration, having the following structural formulae:



Dextro-tartaric acid. Levo-tartaric acid.

These formulae, it will be noticed, differ only in the relative arrangement of their component units, one being the mirror image of the other.

Racemic-tartaric acid consists of a mixture of these two acids in equimolecular proportions. If a dilute solution of racemic-tartaric acid is exposed to the action of *Penicillium glaucum*, the acid is split, the dextro form being consumed while the levo form remains in solution.

Later workers have shown numerous instances where the dextro forms of glucose, mannose, galactose and fructose are consumed by various kinds of micro-organisms while the levo forms are not affected. When *Penicillium glaucum* acts upon mandelic acid (racemic), however, the levo form is consumed and not the dextro. On the other hand, when the same solution is acted upon by *Saccharomyces ellipsoideus* the dextro form but not the levo is consumed.

This selectivity and specificity shown by many species of fungi is to a large extent explained on a basis of enzyme action, the specificity of which is too well known to discuss here.

Dox (6), who has made a careful study of the enzymes of Penicillium and Aspergillus, calls attention to the marked chemical and physiological differences in strains of Penicillium answering the same morphological description. Numerous cases of specificity are described and in regard to the constancy of this action he concludes that, "There is no evidence that enzymes not normally formed by the organism in demonstrable quantities can be developed by special methods of nutrition."

Schellenberg (17) also describes two strains of *Penicillium glaucum* which are morphologically similar but show marked specificity for different hemicelluloses. Several other fungi are also described showing a corresponding specificity of action on hemicellulose.

Many similar examples involving slight differences in molecular configuration could be mentioned, all of which point to a specific relationship between these differences and the protoplasmic structure and nutritive mechanism of the organisms.

It is interesting to note in this connection the recent work of Knudson (10) in which he shows that galactose and mannose are toxic to certain green plants, while glucose, sucrose and other sugars are readily assimilated.

Just what are the specific food requirements of the biologic forms of stem rust under discussion is of course not known and perhaps will never be known until we understand better the intimate metabolism of the plant cell, or until we succeed in growing rusts on artificial synthetic media. Whatever they may be, from our general knowledge of obligate parasitism we are justified in assuming that they are more specific than those of facultative parasites or saprophytic fungi.

That the required food is an intermediate product of cell metabolism and is a carbohydrate, or some substance closely related to the carbohydrates, is strongly indicated by the fact that the rusts will not develop on a host deprived of its carbohydrate food supply, while mineral starvation has no appreciable influence on their development. This was shown for *P. glumarum* by Ward (28) and for *P. sorghi* and *P. coronata* by Mains (12), whose work has been verified in part by the writer with the biologic forms of *P. graminis*.

As evidence to justify the second assumption it is only necessary to refer to the work of Reichert (16), on, "The differentiation and specificity of starches in relation to genera, species, etc." In this work Reichert proves conclusively that starches exist in plants in different stereoisomeric forms that are specifically modified in relation to varieties, species and genera. In his own words, "The history of starch from the moment of the utilization of carbon dioxide and water to form an aldehyde, through the various steps of synthesis of monosaccharoses, disaccharoses, and polysaccharoses to the ultimate appearance of starch, and the reversal of these steps when the starch is consumed as food, is upon logical grounds conceived to be one of continuous and consecutive enzyme action. The enzymes synthesize starch and its precursors and no other substances, because they can build up only such chemical structures as have configuration complementary to themselves, each tending naturally to build those forms which have the closest configuration; and likewise each analyzes only such substances as have the same stereochemic relationship. If, as stated, protoplasm uses only such organic substances as have a complementary stereochemic form, it follows as a corollary that starch has a corresponding configuration, and that if starch has such a conformable structure so must have the enzymes that produce it. In other words every

enzyme formed by any given protoplasm is specifically produced to carry out operations which are directly or indirectly essential to the existence of protoplasm itself and must *ipso facto* bear a stereochemic relationship to its mother substance; therefore, protoplasm, enzyme, and product have in common the same fundamental stereochemic peculiarities. In fact as the results of these researches go to show, every synthetic organic substance produced by any given protoplasm through the agency of its enzymes has a configuration in agreement with that of the protoplasm. If, as must be admitted, corresponding kinds of protoplasm in different organisms differ, the corresponding synthetic metabolites will differ, and, conversely, if the latter differ, so must the former. Hemoglobins, which are corresponding substances, have been shown to differ in specific relationship to genera and species; and the same extraordinary phenomenon has been brought to light in respect to starches."

In this work the starches of over three hundred species of plants were studied and abundant evidence is presented to justify the above statement. It is important to note in this connection that Reichert (16, p. 376), on the basis of starch peculiarities, has divided the type hosts of the biologic forms of *Puccinia graminis* into two distinct groups corresponding with the classification of the biologic forms on the basis of parasitism by Stakman and Piemeisel (21, p. 492) and on morphological characters by Stakman and Levine (23a).

In addition to these two assumptions it is necessary to explain the injurious effect of the invading fungus on the cells of resistant plants. It is well known that fungi, in the absence of readily available food, secrete certain enzymes in much larger quantities than they do under normal conditions. A case of this kind has been described by Cooley (4) in which *Sclerotinia cinerea* secreted a cellulose hydrolyzing enzyme when grown on filter paper with no other nutrient supplied, but when small quantities of peach juice or other soluble carbohydrates such as glucose were added, no cellulose hydrolysis occurred. Is it not logical to assume that it is these enzymes, secreted in excess only when the fungus fails to find abundant readily available food, which are injurious to the plant cells?

With this evidence for the justification of the above assumptions the following hypothesis is offered to explain the facts of resistance as observed in this work and in that of previous workers: Each biologic form of rust has its specific food requirements, conforming with the molecular configuration of its protoplasm. This food, which is in turn specific in relation to the protoplasm which produces it, is found only in a limited number of host species. When a given biologic form of rust invades a plant which does not contain this specific food the fungus consequently dies of starvation and in this process of starvation secretes an enzyme which is injurious to the plant cells with which it comes in contact.

This hypothesis would seem to explain the observed facts better than any previously offered. It does not require the assumption of the universal presence of specific toxins and anti-toxins, for the existence of which we have no evidence, even in resistant hosts in the immediate region of infection. On the other hand, there is abundant evidence to justify the assumption of specific food relations between host and parasite.

This hypothesis, although supported by very little original experimental evidence, is offered as a possible explanation of the facts of rust-resistance and also of biologic specialization, two probably identical phenomena.

SUMMARY

1. The infection capabilities of the two biologic forms of rust studied on 72 varieties of wheat show that: (1) *P. graminis tritici-compacti* has a narrower host range than does *P. graminis tritici;* (2) as a rule the hard spring wheats are resistant to *P. graminis tritici-compacti,* while the soft winter wheats are susceptible; (3) the hard winter wheats show varying degrees of resistance to *P. graminis tritici-compacti;* and (4) no one of these groups of wheats as a class is resistant to *P. graminis tritici.*

2. The action of the two biologic forms is distinctly and consistently different on the following varieties: Royalton (Minn. 1037), Marquis (Minn. 1239), Barletta (Minn. 1178), Turkey (Cosgrove, Minn. 529), Crimean (Kan. P 765), Alberta Red (Kan. 2048), Red Winter (Kan. 196), Turkey (Kan. 2126), Turkey (Kan. 2039), Beloglina (P 750), Bearded Fife (Kan. 2049), Kanred (P 762), P 1066, P 1068 and P 2141. These varieties are differential hosts for the two biologic forms of rust.

3. *Puccinia graminis tritici-compacti* seems to be a distinct and constant biologic form which cannot be changed easily by means of host influences.

4. The following hypothesis is offered to explain the phenomena of rust resistance and biologic specialization in rusts: Each biologic form of rust has its specific food requirements, conforming with the molecular configuration of its protoplasm. This food, which is in turn specific in relation to the protoplasm which produces it, is found only in a limited number of host species. When a given biologic form of rust invades a plant which does not contain this specific food the fungus consequently dies of starvation and in this process of starvation secretes an enzyme which is injurious to the plant cells with which it comes in contact.

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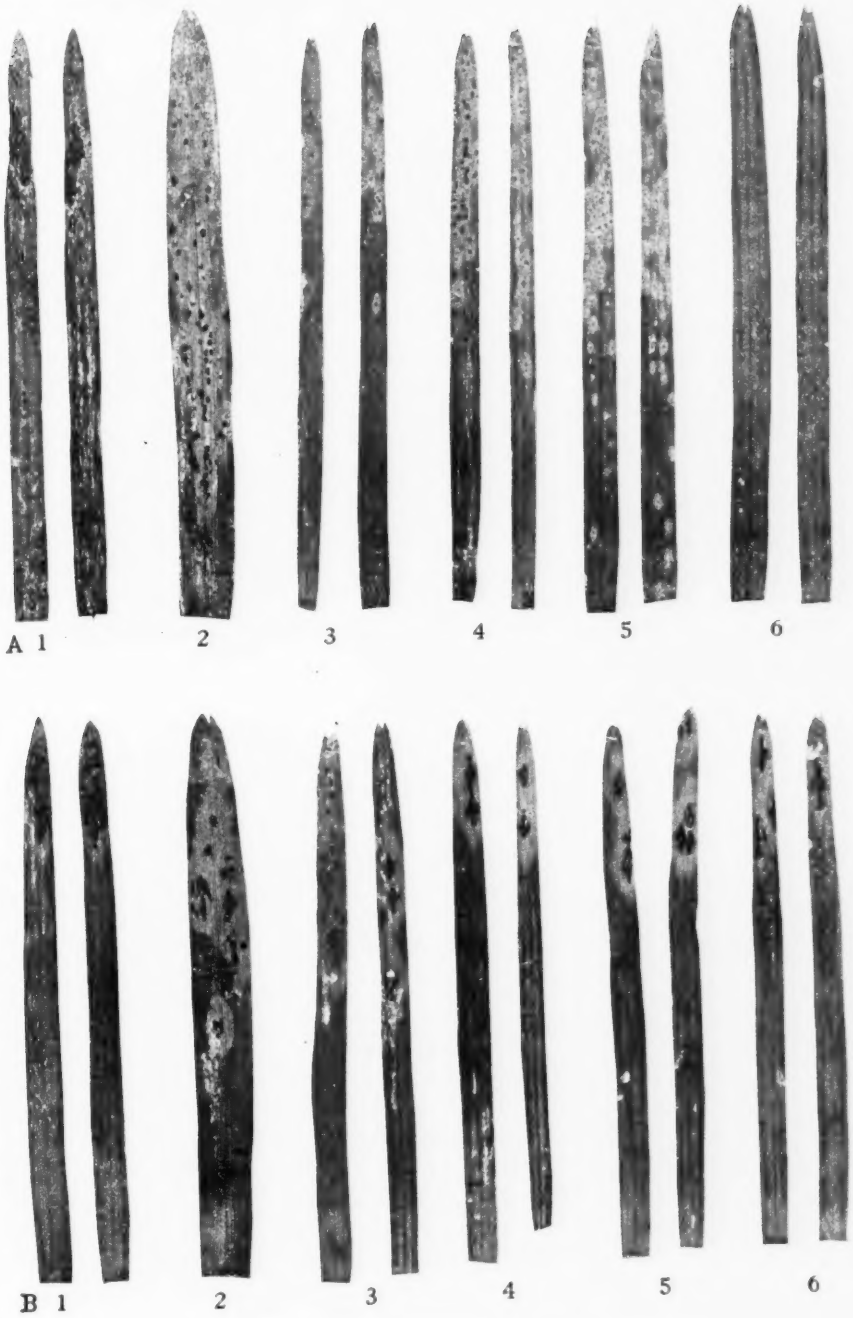
PLATE IV

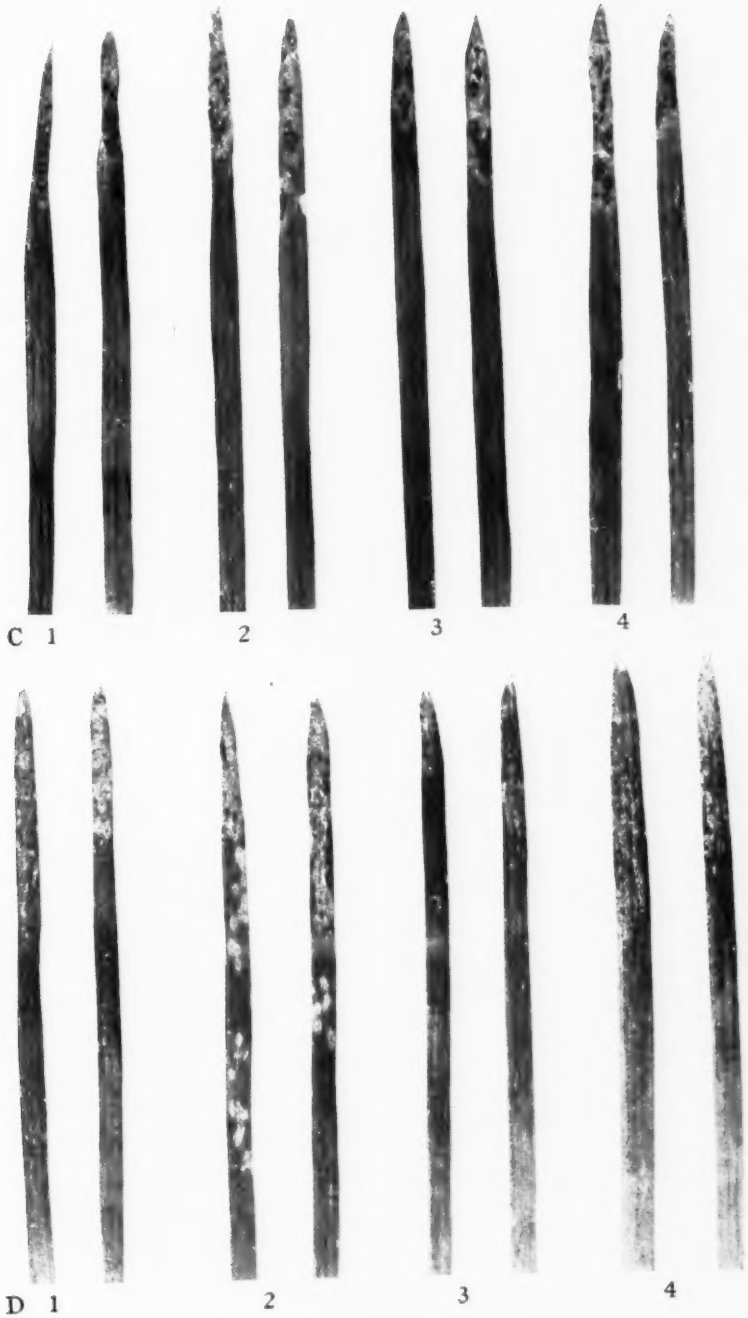
(A) *P. graminis tritici-compacti* and (B) *P. graminis tritici* on: *1;* Club Wheat (Brown Gloria); *2*, barley (Manchuria Minn. 105); *3*, Haynes bluestem Minn. 169; *4*, Royalton Minn. 1037; *5*, Marquis Minn. 1239; and *6*, Parletta Minn. 1178.



LEACH: PARASITISM OF PUCCINIA

PLATE V

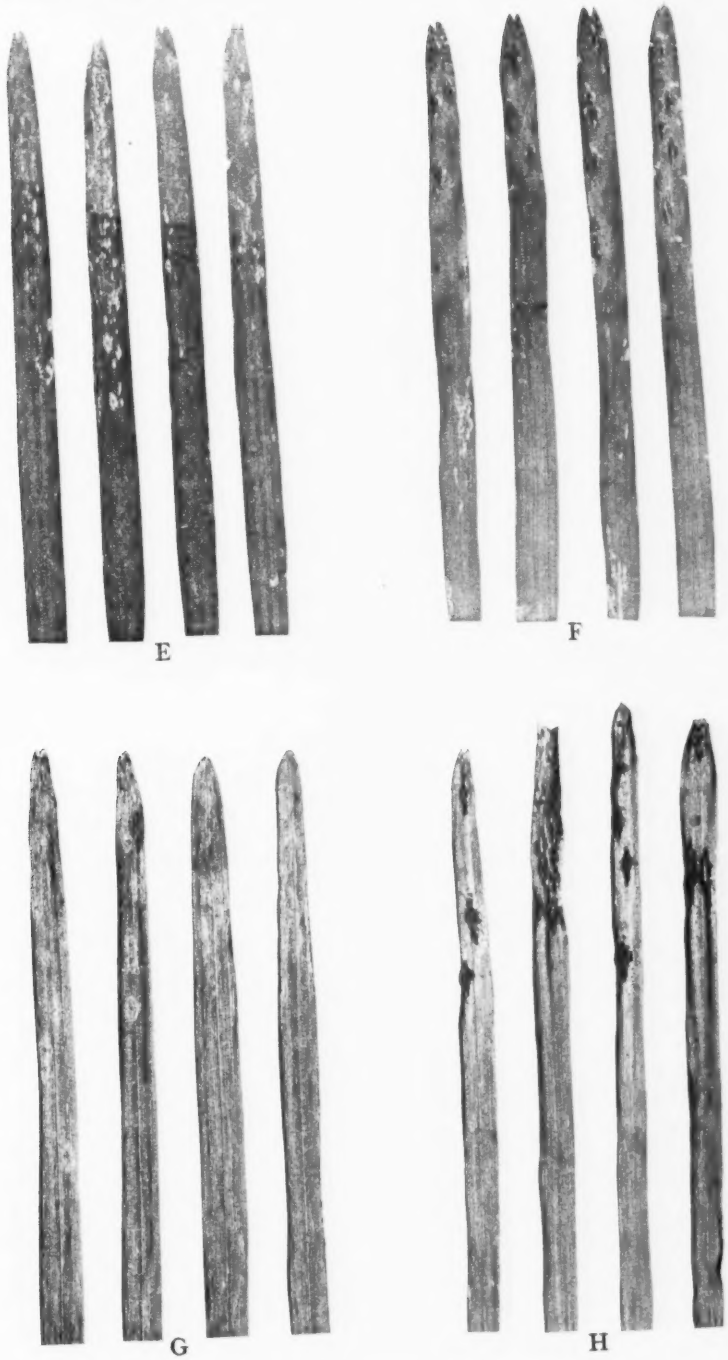
P. graminis tritici-compacti on (C) varieties of soft winter wheat: *1*, Fulcaster; *2*, Purple Straw; *3*, Red May; *4*, Golden, and (D) varieties of hard spring wheat: *1*, Marquis; *2*, Royalton; *3*, Mindum (durum); *4*, Speltz Marz (durum).



LEACH: PARASITISM OF PUCCINIA

PLATE VI

(E) *P. graminis tritici-compacti*, and (F) *P. graminis tritici* on Barletta Minn. 1178. (G) *P. graminis tritici-compacti*, and (H) *P. graminis tritici* on Marquis Minn. 1239.


E
F
G
H

RHIZOCTONIA IN LAWNS AND PASTURES

C. V. Piper and H. S. Coe[1]

With Plates VII and VIII

The general occurrence of *Rhizoctonia solani* on many perennial grasses as well as on accompanying weeds in lawns and pastures is important as it illustrates a feature of this destructive fungus which has heretofore escaped detection. The damage caused to fine plots of turf is often very serious and the injury to pastures and perhaps meadows is doubtless in its entirety very large. Incidentally the general occurrence of this fungus in grass lands complicates greatly the possibility of control methods based on rotations.

In the summer of 1913 our attention was called to a trouble affecting the turf on putting greens of a golf course near Philadelphia. The symptoms were brown spots, varying from a few inches to a foot or more in diameter, which appeared more or less abundantly scattered through the turf. As the trouble was more serious on certain rather moist greens, the conclusion was reached at the time that it was primarily due to poor drainage. Previous applications of lime and fertilizers had not shown any indication that they were helpful. The thorough drainage of two of the greens by tiling resulted in the turf being much better in 1914 and subsequently, but did not entirely obviate the trouble.

In 1914 similar brown spots appeared on the red fescue in the turf experiments of Mr. Fred W. Taylor near Philadelphia. On this course the spots were circular in outline and grew centrifugally, in many cases merging in large areas. During July and August these spots appeared as if dead, but in the cool weather of fall most of them recovered. The definiteness of the spots and their concentric growth at once suggested an organism, but examination by several pathologists did not disclose the causal agent.

In 1916 complaints came from various sources, and the disease was found abundantly about Washington. (Plates VIII and IX.) Careful observation disclosed the fact that early in the morning a fine white mycelium could be seen covering new spots. Later in the day the spots become brown, but in cases where they are actively growing the border is often

[1] Mr. Coe died October 25, 1918. This article has been written entirely by the senior author. The investigations, however, were joint, and in preparing the article, free use has been made of the notes written by Mr. Coe.

sharply marked by a narrow zone of dark smoky green where the grass leaves are dying. Nearly all of the spots attain a definite size, varying from a few inches to 2 feet in diameter, and then cease spreading. In other words, the disease is to some extent self-limiting. Careful examination of the brown spots reveals small black sclerotia, usually on the stems of the grass, often under the sheaths. Cultures were made from the sclerotia and from the free aerial mycelium, which latter is easily obtainable by putting a piece of diseased turf in a moist chamber or under a bell jar. A piece of the turf from the edge of a diseased spot is most satisfactory, and on this the mycelium is abundantly developed in a moist chamber. The cultures of the fungus left no doubt as to its identity with *Rhizoctonia solani*. The organism grows very rapidly in culture media of various kinds, especially on sterilized bean pods and potato plugs. Sclerotia are produced in abundance in cultures, and these compare closely with those produced on different species of grasses and coarse weeds under field conditions.

Among the lawn plants attacked, in the approximate order of their susceptibility, are mouse-ear chickweed (*Cerastium vulgatum*), stitchwort (*Stellaria graminea*), red fescue (*Festuca rubra*), redtop (*Agrostis palustris*), velvet bent (*Agrostis canina*), carpet bent (*Agrostis stolonifera ?*), Rhode Island bent (*Agrostis tenuis*), rough-stalked meadow-grass (*Poa trivialis*), Kentucky bluegrass (*Poa pratensis*), yarrow (*Achillea millefolium*), and veronica (*Veronica serpyllifolia*).

Frequently, especially in the case of mouse-ear chickweed, the disease does not spread beyond the boundaries of the plant, but in other cases a single spot may involve plants of several species. Bermuda grass, white clover, and crab grass seem to be immune.

In 1917 a considerable number of inoculation experiments were made with pure cultures of the aerial mycelium, and in all cases these were successful and produced spots in turf similar in appearance to those from which the organism was isolated. These inoculating experiments were carried out both under greenhouse conditions and under field conditions.

Close observations of this disease during three years at Washington have disclosed the following facts. The disease appears with the first hot, muggy weather of summer. In 1917 it first appeared at Washington on June 13; in 1918 on May 30 in a few spots but not in abundance till July 12. The organism spreads most rapidly during warm, moist weather. With the appearance of dry, hot weather and a lessened amount of dew the disease is greatly checked. With the reappearance of moist, hot weather many new spots appear, and some, at least, of the older ones continue to spread. Practically all of the spots remain brown until the cool weather of autumn, when the greater part of them recover, at least on the mixed

turf that occurs on putting greens. While the disease is most conspicuous on closely clipped turf, it occurs generally in lawns and pastures. It is evident that the damage to pastures is considerable; but as the disease is most abundant during the season when crab grass and other summer grasses are vigorous, it is to a large extent concealed.

In 1917, in an attempt to control the disease in fine turf, experiments with Bordeaux mixture were conducted on a putting green. The first appearance of the disease was on June 13, and on June 15 an area 40 by 80 feet in size was watered with 300 gallons of half-strength Bordeaux mixture, a small portion of the turf being left untreated as a check. No injury whatever resulted to the grass from the use of the Bordeaux mixture. The treated portion seemed to improve very quickly and within a week but few spots were visible. The untreated portion, however, continued to deteriorate, and on July 9 was in very bad shape, while the treated portion then showed no evident sign of the disease. However, the disease again became rampant on the treated area about July 15, when it was again treated with Bordeaux, but the results following this application were by no means as marked as those following the first application. It would seem probable that the disease can be held in check by heavy applications of Bordeaux mixture applied at short intervals from the time the disease makes its first appearance. It is probable that these treatments would have to be made about every three weeks, but the expense of this is excessive, especially in view of the fact that nearly all of the untreated turf recovers in the fall. The difficulty with the use of Bordeaux or any similar fungicide is that as soon as it has been washed from the surface of the grasses the fungus starts a new growth on the grass, unaffected by the Bordeaux mixture on the surface of the soil or on the old stems of the grasses.

On the turf plots at Arlington Farm various chemicals were used in the hope that one might be found to control the disease. Among the substances tried were mercuric bichloride, Bordeaux mixture, sulphur, and iron sulphate. None of these substances proved satisfactory. The sulphur where applied liberally killed the grass completely, and iron sulphate in even very weak solutions was highly injurious. From the fact that the fungus lives over winter as sclerotia, it would seem very doubtful if any satisfactory fungicide control of the disease in turf will be discovered. The most promising line of attack is in securing fine turf grasses which are resistant to the disease.

In this connection experiments have been under way at Arlington Farm for three years, in which pure cultures of many different grasses are under trial. The relative susceptibility of the bent grasses, which are particularly subject to the disease, is interesting and encouraging. Pure vegeta-

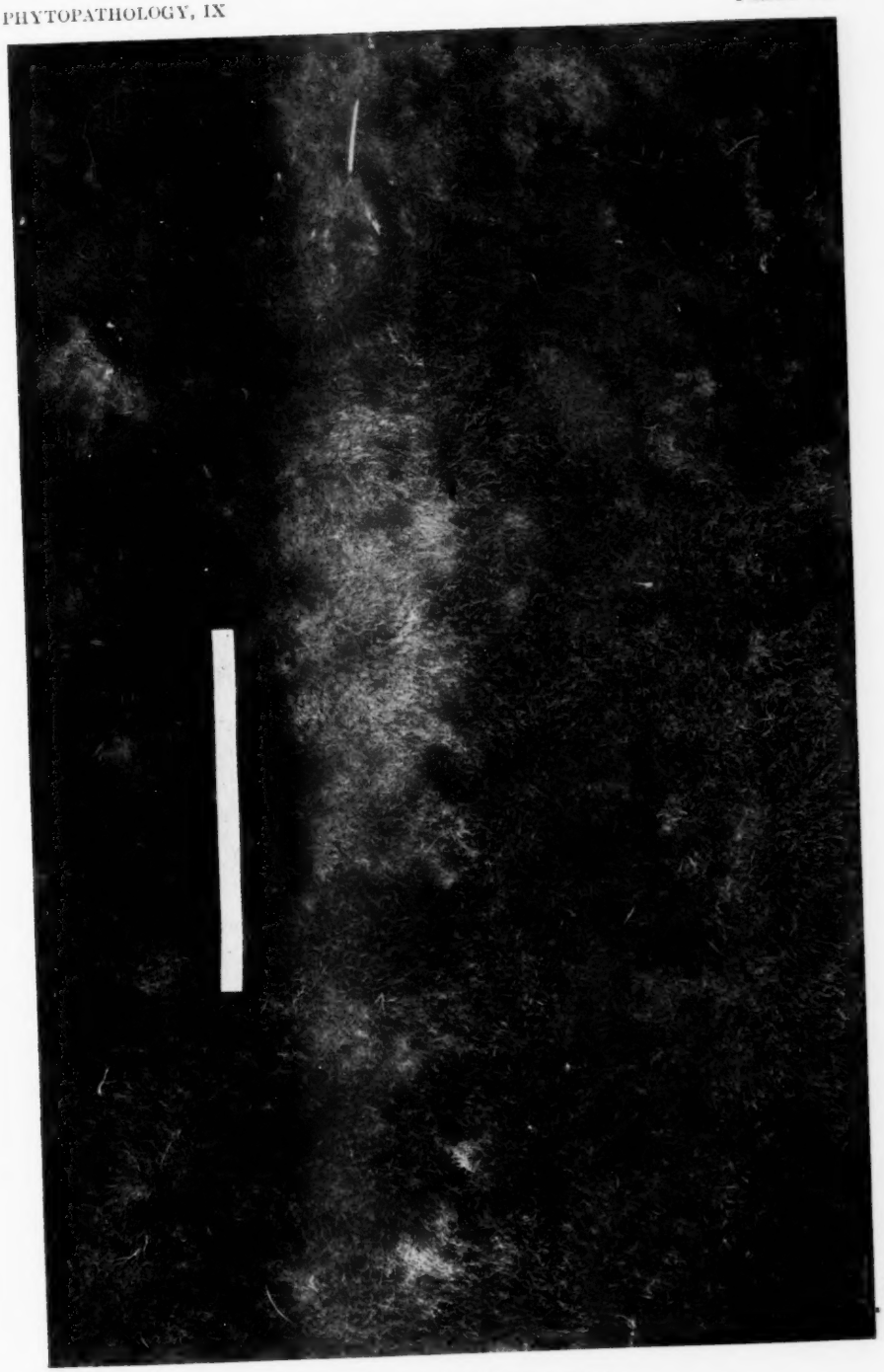
tive cultures of many different strains of velvet bent (*Agrostis canina*) and of carpet bent (*Agrostis stolonifera ?*) have been tested. Some of these strains were completely destroyed by the disease in 1917, and again, in 1918, but one strain of velvet bent is almost completely resistant, and several of carpet bent are highly resistant.

In the course of field studies, the disease has been observed, or specimens have been received, from Poland Springs, Me., Boston, Mass., Kingston, R. I., the vicinity of New York City, Philadelphia, Washington, Chicago, and Minneapolis. The disease is probably of general occurrence in lawns and pastures throughout the northeastern quarter of the United States. Its general occurrence on turf grasses will be of interest to all concerned in the study of this disease on other crops.

Very few references to the occurrence of Rhizoctonia on grasses are on record. Mr. R. J. Haskell, of the Plant-Disease Survey, informs us that *Corticium vagum*, the mature stage of *Rhizoctonia solani*, was reported from Wright County, Minn. on corn in 1916, and *Rhizoctonia napi* on oats is referred to in Internat. Rev. of Sci. and Practice of Agric. Year VII, No. 1, Jan. 1916: 156–8. It seems highly probable that further studies will reveal the occurrence of Rhizoctonia on a large number of grass species.

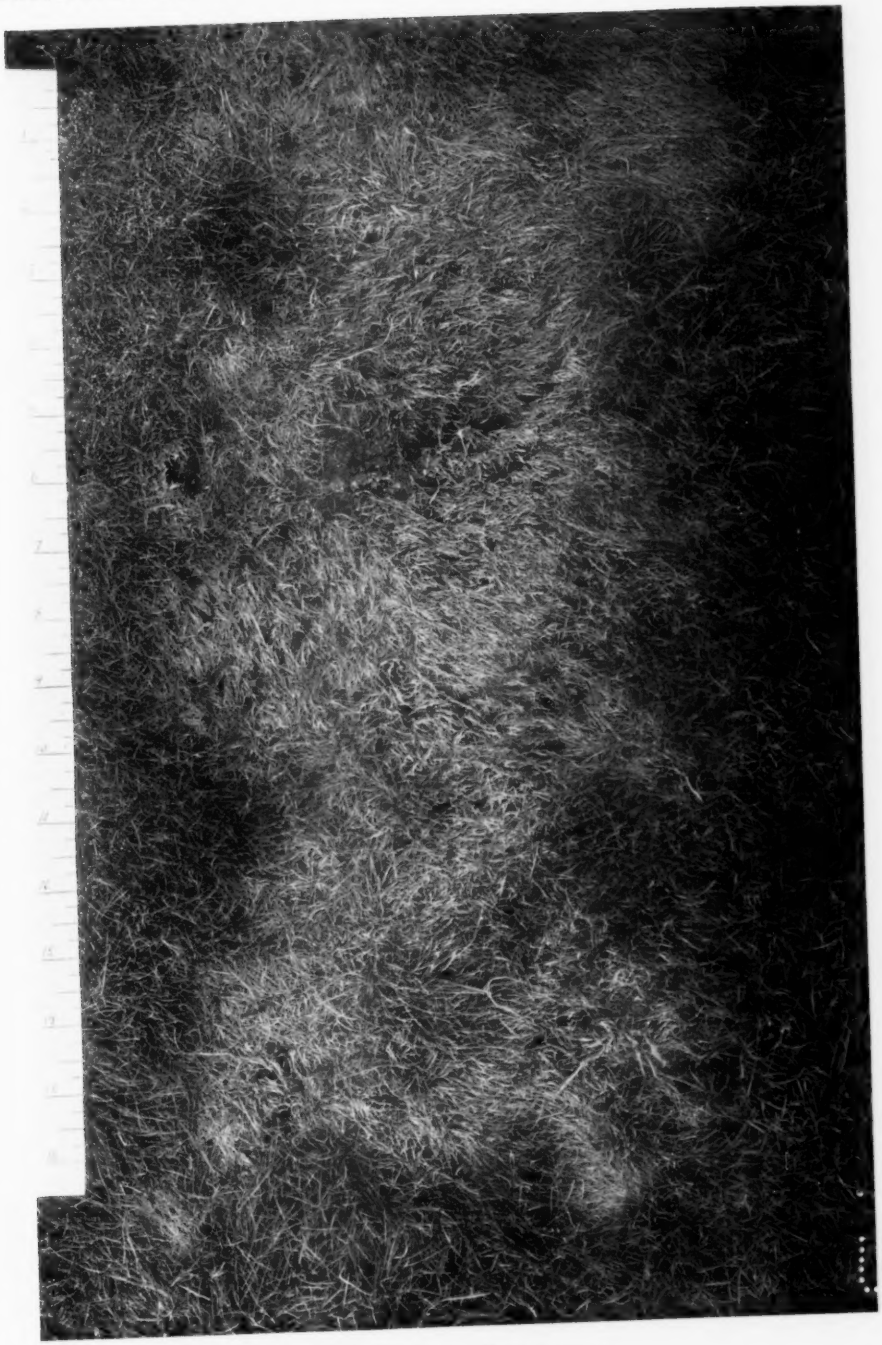
BUREAU OF PLANT INDUSTRY
WASHINGTON, D. C.

PLATE VII. RHIZOCTONIA ON GERMAN MIXED BENT, ARLINGTON FARM, VIRGINIA, JULY, 1917, SHOWING GENERAL CHARACTER OF THE INJURY CAUSED



PIPER AND COE: RHIZOCTONIA

PLATE VIII. RHIZOCTONIA ON GERMAN MIXED BENT. A CLOSER VIEW OF THE SPOT SHOWN IN PLATE 8



PIPER AND COE: RHIZOCTONIA

EXPERIMENTS ON THE CONTROL OF THE ROOT-KNOT NEMATODE, HETERODERA RADICICOLA (GREEF) MUELLER

I. The Use of Hydrocyanic-Acid Gas in Loam Soil in the Field

L. P. Byars

With Plate IX

INTRODUCTION

The urgent need of some widely applicable and effective means of eradicating the common nematode, *Heterodera radicicola* (Greef) Mueller, from infested soils caused the writer in 1916 to begin experiments which were designed to test the efficiency of hydrocyanic-acid gas for this purpose. Since that time these experiments have been in progress both in the pathological greenhouses at Washington, D. C., and out-of-doors at the Plant Introduction Station[1] of the United States Department of Agriculture, at Brooksville, Florida. This paper deals with the results obtained in loam soil at the latter place, where the investigations are being continued on light sandy soil only. Data secured from the greenhouse work will be reported at a later date.

In Europe and America for many years a wide range of solid, liquid, and gaseous chemicals, as well as commercial fertilizers, have been experimentally tested for their value as soil disinfectants for the root-knot nematode or for other soil nematodes parasitic on plants. As a rule, results secured from these tests have been negative, and none of these chemicals or fertilizers has proved fully effective and at the same time entirely satisfactory in eliminating plant parasitic eelworms from loam soil in the field. The truth of this general statement is borne out by the early efforts of the European investigator Hollrung (4) and of such American workers as Neal (6), Stone and Smith (7), and Atkinson (1). The assertion also finds support in the later careful investigations of Bessey (2) and the more recent work of McClintock (5) and Watson (8). Cognizant of the generally negative results obtained by these and other investigators, the writer decided to determine the possibilities of hydrocyanic-acid gas for killing nematodes because of its well known fumigating qualities in greenhouses, orchards, dwellings, etc. Furthermore no reports of its use as a soil dis-

[1] The writer wishes to express his appreciation of the cordial coöperation and assistance in initiating and carrying out these investigations given by members of the Office of Foreign Seed and Plant Introduction, Bureau of Plant Industry, especially Mr. R. A. Young.

infectant for the root-knot nematode have been seen. DeOng (3), however, has recently published some important data on its value as a fumigant for soil insects and its effect on germinating seeds and plants.

EXPERIMENTS OF 1916

The experiments of 1916 were carried out on a small field of fairly heavy, dark, loam soil—the so-called hammock land of Florida—located near the center of the Plant Introduction Station of the United States Department of Agriculture, at Brooksville, Florida. This soil was well infested with nematodes, as shown by observations made in 1915. A crop of Trinidad dasheens, *Colocasia esculenta* (L.) Schott, growing on the land at that time proved to be almost a complete failure because of root-knot and the writer by careful examination of the roots of each plant found 100 per cent of them infected with nematodes. The dasheen, a variety of the Oriental taro, is a valuable starchy root crop, widely grown as a staple food throughout the tropics and recently introduced into commercial cultivation in the Southern States.

Isolation of plots. To obtain reliable data on the effect of hydrocya ic-acid gas or any other chemical on nematode infested soil it is, of course, absolutely necessary that treated areas be so isolated as to prevent or reduce to a minimum the opportunities for reinfestation. A failure to properly isolate experimental plots in the field has no doubt in many instances led to the wrong interpretation of results obtained in working with nematodes. Consequently in carrying out the experiments reported here the author has employed a method of isolating and handling field plots which he feels has yielded dependable data. A description of the method follows.

The infested area used in the experiment was divided into three rows of plots 5 feet apart, each row consisting of nine plots. These plots were numbered from 1 to 27, inclusive, as shown in the accompanying diagram.

Diagram of isolated plots used in hydrocyanic-acid gas experiments of 1916–1917

1	4	7	10	13	16	19	22	25
1½sd	3sd	6sd	9sd	Check	1½sd	9sd	6sd	3sd
s+ s+	med+ s+	− −	− m+	s+ s+	m+ s+	− vm+	− s+	med+ s+
2	5	8	11	14	17	20	23	26
1½sd	3sd	6sd	9sd	Check	3sd	1½sd	9sd	6sd
s+ s+	m+ s+	− −	− vm+	s+ s+	− m+	m+ s+	− m+	− s+
3	6	9	12	15	18	21	24	27
1½sd	3sd	6sd	9sd	Check	6sd	3sd	1½sd	9sd
− med+	m+ s+	− −	− −	s+ s+	− m+	m+ s+	s+ s+	− med+

The diagram shows the arrangement and treatment of plots; also the occurrence and extent of root-knot on dasheens which were grown in them.

Each rectangle of the diagram represents a plot, which is numbered at the top.

The treatment of the plots is indicated by the symbols $1\frac{1}{2}$, 3, 6 and 9 sd, which represent multiples of the standard rate of application of the chemicals, viz., 400 pounds of sodium cyanide and 600 pounds of ammonium sulfate per acre.

Presence or absence of root-knot is represented by plus (+) and minus (−) signs, which are placed in the lower left and right corners for results of 1916 and 1917, respectively.

The abbreviations s. (severe), med. (medium), m. (mild), or vm. (very mild) placed before these plus or minus signs indicate the degree of infection found on the test crop, dasheen, grown in each plot.

Individual plots, approximately 4 by 8 feet in size, were isolated on all sides by means of galvanized sheet iron of no. 24 gauge, which was sunk into the soil about 16 inches, or 6 inches below the hard pan, and extended above the ground surface about 20 inches. By crimping the iron and bolting the sides and ends together an almost water-proof and hence virtually nematode-proof joint was secured. Thus an entrance of the parasites through the soil was prevented on all sides to the depth of the iron, and as nematodes do not penetrate into, or live in the heaviest, most compact soils, it is highly improbable that they could pass down under the bottom of the galvanized iron and enter the plots. Above ground the possibility of spreading nematode-infested soil or other material onto the plots by such agencies as the spattering action of rain, the movement of surface water, and the tramping of men and animals was reduced to a minimum by the high iron walls. To eliminate further the possibility of spreading the parasite by animals, such as rabbits, chickens, etc., a 5-foot, closely woven wire fence was placed about the entire experimental area. The isolated plots ready for chemical treatment are shown in plate I, figure 1.

Treatment of plots. Treatment of the plots was accomplished by applying various amounts of sodium cyanide and commercial ammonium sulphate to the soil in both the powdered and liquid state, hydrocyanic-acid gas being liberated as indicated by the formula: $2\,NaCn + (NH_4)_2SO_4 = 2HCn + Na_2SO_4 + 2NH_3$. As preliminary work by Mr. F. A. Kaufman[2] of the Roessler and Hasslacher Chemical Company had indicated that 400 pounds of NaCn and 600 pounds of $(NH_4)_2SO_4$ per acre killed certain soil fungi and insects, these quantities were chosen by the writer as standard rates of application. One and one-half, two, three, six, and nine times this standard were used in the plots. The chemicals in pow-

[2] As reported in conversation with the writer.

dered form were applied successively to the soil. Each application was spaded in to a depth of about 6 to 8 inches and the plots well soaked with water. The chemicals were also applied in liquid form, each being dissolved in 10 gallons of water and successively poured on the plots. In order to allow the poisonous gas to escape from the soil, various lengths of time, from two to five weeks, were allowed to elapse between the chemical applications and the planting of the inclosed areas. In some plots the soil was undisturbed before planting, while in others it was spaded. Well water was poured on the plots used as a check. Complete details as to the method of treating and handling the isolated areas are given in table 1.

Planting and cultivation of plots. After the desired lengths of time had elapsed following the treatment, six selected nematode-free dasheen tubers of the Trinidad variety were planted in each plot, no fertilizer or manures being added. Dasheens were used as a test crop because they are very susceptible to nematodes and because they occupy the ground for a full season and thereby afford the maximum opportunity for infection. Cultivation and weeding were done at weekly intervals until harvest by a responsible gardener, who disinfected his hoe or other implements with copper sulphate before using them in any plot; it was not necessary to step on the plots because of their narrowness. Weeds were scrupulously kept from the entire fenced area, thus preventing propagation of the nematode, except on the dasheens, for a distance of 5 feet beyond as well as within each plot.

RESULTS OF 1916 EXPERIMENTS

At the end of the growing season the dasheens in each plot were removed, especial care being taken to lift as many roots and rootlets as possible along with the corms and a careful macroscopic, and whenever necessary microscopic, examination made for nematode infection. The number and per cent of plants found infected are recorded in table 1, while the extent of infection, whether mild, medium, or severe, is indicated in the diagram by appropriate symbols placed in the lower left corner of each plot.

An analysis of table 1 shows that of the 35 plants grown in the 6 plots, nos. 1, 2, 3, 16, 20, and 24, treated with $1\frac{1}{2}$ times the standard amount of chemicals, 19 plants, or 54 per cent, were diseased, while out of the same number of plants in the 6 plots, nos. 4, 5, 6, 17, 21, and 25, receiving 3 times the standard amount of chemical, 12 plants, or 34 per cent, showed root-knot. However, no disease was found on the 30 and 25 plants, respectively, grown in each of 6 plots receiving 6 and 9 times the standard quantity of chemicals. Ninety-four per cent, or 17 out of 18 plants grown in the 3 untreated check plots, nos. 13, 14, and 15, were severely infected

with nematodes. Thus it appears from these figures that while the percentage of plants diseased is perceptibly reduced at both 1½ and 3 times the standard application, the trouble is by no means eliminated. Indeed, the 54 per cent of diseased plants occurring in the 1½ times standard plots were for the most part severely infected, as shown by a study of the diagram, while only mild to medium infection took place on the 34 per cent of infected plants grown in the plots treated with 3 times standard. No root-knot could be found on the dasheens growing in those isolated plots receiving 6 and 9 times the standard unit of treatment and it was tentatively assumed that all nematodes had been killed. But the next season's results showed the error of this assumption.

Even if the higher rates of application had proved permanently effective in preventing root-knot, the cost involved would limit or prohibit the general use of the chemicals, the value of the sodium cyanide alone when applied at the rate of 400 pounds per acre being about $110. However, for controlling the nematode in small areas or in limited quantities of soil where other means of control than chemicals are not readily available, hydrocyanic-acid gas might be used to advantage in spite of the cost involved, since it appears to be more efficient than most chemicals which have been employed for this purpose.

GENERAL OBSERVATIONS

Evidence that the plots were well isolated throughout the course of the experiment is shown by the fact that no nematodes were found at the end of the season on plants in plots adjacent to plots nos. 6, 14, 15, and 20, which were pronouncedly infested with nematodes. This observation is graphically recorded on the diagram. Infection during 1916 is denoted by a plus (+) sign placed in the lower left corner of the plot or lack of it by a minus (−) sign.

Although no records of the crop yields were kept, no decidedly consistent differences in the size of tops and tubers of the dasheen plants were evident between those grown in the check plots and those produced in plots treated with the chemicals at 1½ and 3 times the standard amount. In plots where the larger amounts of the chemicals were applied the dasheens appeared to be reduced in top and tuber size below that found in other plots. Thus the smaller applications seemed to have little, if any, fertilizing effect, while the chemicals in larger amounts appeared to reduce growth and yield. Some idea of the size and vigor of the maturing dasheens may be obtained by examining plate I, figure 2.

There seemed to be no correlation between the amount of disease present in a plot and the method of applying the chemical; that is, the

TABLE 1

Experiments of 1916 with hydrocyanic-acid gas as a soil disinfectant for the root-knot nematode

TREATMENT		PLOT NUMBER	RESULTS				
			Number of plants (dasheens)		Per cent of plants affected with root-knot		
Method of applying chemicals, on May 11, 1916	Amount of NaCn and $(NH_4)_2SO_4$ applied (liberating HCn)		Examined October, 1917	Affected with root-knot	In each plot	In each set of plots	Total average for each treatment
Powdered chemicals successively spaded into the soil and, except in plots 2, 5, 8, and 11, which were again spaded one week later, allowed to stand unmolested for 2 weeks, when 6 dasheens were planted in each plot. A thorough drenching of soil after application of chemicals	1½ times standard*	1	6	6	100	61	54
		2	6	5	84		
		3	6	0	0		
	3 times standard	4	6	3	50	33	34
		5	6	2	33		
		6	6	1	16		
	6 times standard	7	4	0	0	0	0
		8	6	0	0		
		9	5	0	0		
	9 times standard	10	5	0	0	0	0
		11	3	0	0		
		12	5	0	0		
Check. Merely spaded and then drenched with water	Check, no chemical added	13	6	6	100	94	94
		14	6	6	100		
		15	6	5	84		

Chemicals applied as in plot no. 1. Dasheens planted *3* weeks later	$1\frac{1}{2}$ times standard	16	6	1	16		
	3 times standard	17	5	0	0		
	6 times standard	18	4	0	0		
	9 times standard	19	4	0	0		
Chemicals applied as in plot no. 1. Dasheens planted *5* weeks later	$1\frac{1}{2}$ times standard	20	6	2	33	47	
	3 times standard	21	6	2	33	35	
	6 times standard	22	5	0	0	0	
	9 times standard	23	6	0	0	0	
NaCn and $(NH_4)_2SO_4$ each dissolved in 10 gallons water before application. Dasheens planted *2* weeks later	$1\frac{1}{2}$ times standard	24	5	5	100		
	3 times standard	25	6	4	66		
	6 times standard	26	6	0	0		
	9 times standard	27	2	0	0		

* Standard indicates that the chemicals were applied at the rate of 400 pounds NaCn and 600 pounds $(NH_4)_2SO_4$ per acre or 4.5 and 6 ounces, respectively, per plot.

chemical was as effective when applied in the powdered as when used in the dissolved form.

The per cent of tuber germination was not appreciably affected either by a second spading of the soil or by varying the time of planting beyond two weeks after adding the chemicals.

EXPERIMENTS OF 1917

The experiments of 1917 were designed to determine: (1) whether the heavier applications of chemicals at 6 and 9 times the standard rate had eradicated all nematodes from the treated plots or had merely so reduced their number as to permit the growing of disease-free plants on the soil for one season; (2) the progress of the disease in plots receiving the milder chemical treatments; and (3), if the disinfectant had impaired the soil from an agronomic viewpoint. These experiments, therefore, are an extension of those of 1916 and were performed on the same plots. They were carried out as follows:

Following the removal of the dasheen crop in the fall of 1916 the plots were left undisturbed until shortly before planting time next spring. In the spring of 1917 each plot was thoroughly spaded, uniformly fertilized, and again planted to tubers of nematode-free Trinidad dasheens. Subsequently throughout the growing season the plots were cultivated weekly, the same precautions of disinfecting any implements used and otherwise preventing the transfer of nematodes to isolated plots being taken as described for the work of 1916. Likewise, a final examination for nematodes on the below-ground parts of the dasheen plants was made in the fall as was done the previous season. The data thus obtained are recorded in table 2.

RESULTS OF 1917 EXPERIMENTS

One hundred per cent infection occurred in those plots which had received $1\frac{1}{2}$ and 3 times standard treatment, showing a considerable increase over the previous season's figures of 54 and 34 per cent infection for the same plots. As shown in the diagram, infection in these plots was on the average perceptibly more severe than in 1916. The untreated check plots also showed 100 per cent of severe infection. Thus these data indicate that the fumigant used at the stated rates has little if any effect in perceptibly reducing the number of nematodes for more than one season.

An average of 50 and 56 per cent, respectively, of the plants grown in those plots which had been treated with 6 and 9 times the standard amount of hydrocyanic-acid gas were infected as compared with no infection the previous year. While the number of diseased dasheens in these heavily

TABLE 2

Experiments of 1917 with hydrocyanic-acid gas as a soil disinfectant for the root-knot nematode

TREATMENT IN 1916. AMOUNT OF NaCn AND $(NH_4)_2SO_4$	PLOT NUMBER	RESULTS				
		Number of plants (dasheens)		Per cent of plants affected with root-knot		
		Examined October, 1917	Affected with root-knot.	In each plot	In each set of plots	Total average for each treatment.
$1\frac{1}{2}$ times standard*	1	5	5	100	100	100
	2	4	4	100		
	3	4	4	100		
3 times standard	4	3	3	100	100	100
	5	5	5	100		
	6	6	6	100		
6 times standard	7	5	0	0	0	50
	8	5	0	0		
	9	6	0	0		
9 times standard	10	6	5	84	41	56
	11	5	2	40		
	12	4	0	0		
Check, no treatment	13	5	5	100	100	100
	14	5	5	100		
	15	3	3	100		
$1\frac{1}{2}$ times standard	16	4	4	100		
3 times standard	17	4	4	100		
6 times standard	18	6	6	100		
9 times standard	19	3	1	33		
$1\frac{1}{2}$ times standard	20	5	5	100	100	
3 times standard	21	5	5	100	100	
6 times standard	22	5	5	100	100	
9 times standard	23	4	4	100	71	
$1\frac{1}{2}$ times standard	24	2	2	100		
3 times standard	25	5	5	100		
6 times standard	26	6	6	100		
9 times standard	27	5	4	80		

* For full data on the method of treating the different plots in 1916 see table 1.

treated plots was above 50 per cent, yet the degree of infection on the plants as a whole was mild. In fact, only a trace of disease could be found on some plants after a most careful microscopic examination. These data seem to show that even though no root-knot occurred in the plots in 1916,

yet enough of the parasites remained alive in the soil to cause mild infection the next season.

No injurious or retarding effect on the germination or growth of the dasheens due to the disinfectant was observed in any of the treated plots. The yields, however, on treated and check plots alike were very small because dasheens had been grown in them for two years previously.

SUMMARY

Hydrocyanic-acid gas as liberated in loam soil by applications of sodium cyanide (NaCn) and commercial ammonium sulphate ($(NH_4)_2SO_4$) failed to eradicate the root-knot nematode, *Heterodera radicicola*, from the soil, even when these chemicals were applied at the rate of as much as 3600 pounds and 5400 pounds, respectively, per acre.

No infection, however, was found at the end of the first season on dasheen plants grown in plots treated with those quantities, nor in those where two-thirds of the amounts were used; but in the same plots at the end of the second season there was mild infection of about one-half of the plants.

In plots receiving one-third and one-sixth of the above quantities of the chemicals less than half the test plants showed infection the first season, while at the end of the next year every plant grown in these plots was infected.

The chemicals were about equally effective in powdered and liquid form.

Growth of the dasheens was not appreciably increased by the smaller application of the chemicals and, during the first season, was somewhat retarded by the larger treatments.

Thus, on account of the cost and because of the facts presented, hydrocyanic-acid gas does not appear to be a practicable means of controlling root-knot on large areas of loam soil. On a small scale, however, it may be used to advantage, since it seems to be more efficient than most chemicals which have been employed for this purpose.

In obtaining the results here summarized field plots of soil have been isolated and subsequently handled by a method which prevents or reduces to a minimum the possibility of reinfestation by the root-knot nematode. The method appears to be equally well adapted for use in experimenting with other soil organisms parasitic on plants.

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PLATE IX

FIG. 1. Photograph of the experimental plots showing manner of isolating them before treatment with chemicals.

FIG. 2. Isolated experimental plots at the end of the growing season, containing the test crop, dasheen.

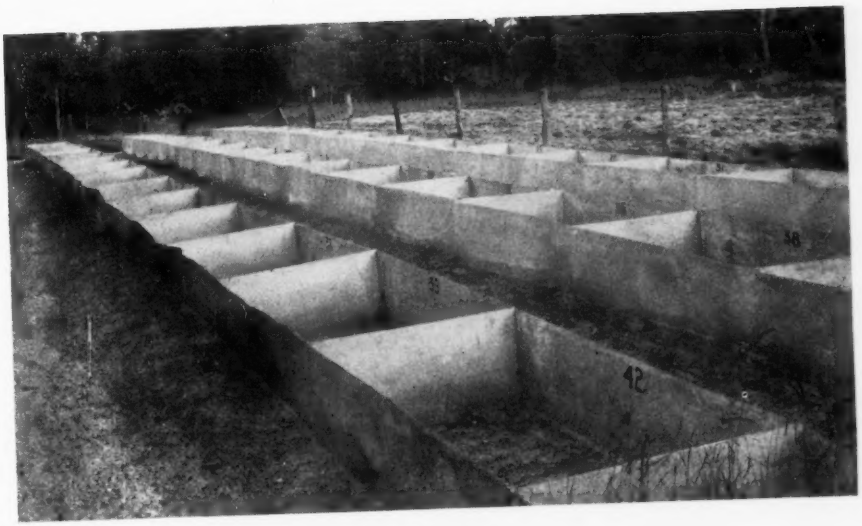

FIG. 1

FIG. 2

PHYTOPATHOLOGICAL NOTES

Personals. Mr. Wm. B. Brierley of the Pathological Laboratory, Royal Botanic Gardens, Kew, and formerly lecturer in economic botany to Manchester University, has accepted the appointment of mycologist to the new Institute of Phytopathological Research, Rothamsted Experimental Station, Harpenden, England.

Mr. L. H. Leonian has accepted the position of assistant professor of biology in the New Mexico College of Agriculture recently made vacant by the resignation of Mr. F. C. Werkenthin. Mr. Leonian was employed during the past summer by the Plant Disease Survey Office of the Bureau of Plant Industry, and previous to this was research assistant in horticulture at the South Carolina Agricultural Experiment Station.

Miss Helen E. Fox of Jackson, Michigan, has been appointed plant pathologist in the Laboratory of Plant Pathology, U. S. Department of Agriculture.

Mrs. Eleanor H. Batson, a graduate student in the University of Missouri, has been appointed assistant pathologist in the Office of Sugar Plant Investigations, Bureau of Plant Industry.

The following workers have been added to the staff of the Office of Cereal Investigations, Bureau of Plant Industry:

Dr. Arthur T. Evans, formerly a graduate student at the University of Chicago but more recently employed as a leader in the control of cereal smuts, has been given a permanent appointment in general disease investigations.

Mr. E. H. Toole, formerly instructor in plant pathology at Purdue University, has been appointed assistant pathologist and will take up work on corn diseases, with headquarters at LaFayette, Indiana.

Mr. John W. Baringer, a student at Wabash College, has accepted a position as assistant pathologist in the barberry eradication campaign, with headquarters at Crawfordsville, Indiana.

Dr. James A. Faris, lately professor of botany and bacteriology at St. Joseph's Union College, St. Joseph, Missouri, has become pathologist in the barberry eradication campaign, with headquarters at Lincoln, Nebraska.

Dr. Vern Bonham Stewart, formerly assistant professor of plant pathology at Cornell University and more recently pathologist in the Department of Agriculture engaged in markets inspection work on vegetables, died of pneumonia following influenza, in New York City, December 3, 1918.

Mr. Charles S. Ridgway died of pneumonia, at his home in Baltimore, Maryland, December 8, 1918. Mr. Ridgway had been an employe of the Bureau of Plant Industry during the past five years, first as assistant in botanical laboratory work in the Office of Tobacco Investigations, and since May, 1918, as assistant pathologist in the Office of Cotton, Truck, and Forage Crop Disease Investigations, engaged in extension work on the control of truck crop diseases in Maryland. He was a graduate of the Maryland Agricultural College.

Howard Sheldon Coe, assistant agronomist in the Office of Forage Crop Investigations, Bureau of Plant Industry, died October 25, 1918, at Beaumont, Texas, from pneumonia following influenza. Mr. Coe was a graduate of Iowa State College, from which institution he received the degree of M.S. in Agriculture in 1915. While a student there he was assistant instructor in botany for a portion of his time during three years. In 1913 he was appointed consulting botanist and plant pathologist at the South Dakota Experiment Station, which position he held until he entered the service of the U. S. Department of Agriculture in July, 1914, as scientific assistant in forage crops. His most recent studies were mainly in connection with sweet clover, velvet beans, and the problems of permanent pastures in the South.

LITERATURE ON PLANT DISEASES[1]

COMPILED BY EUNICE R. OBERLY, LIBRARIAN BUREAU OF PLANT INDUSTRY AND FLORENCE P. SMITH, ASSISTANT

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All authors are urged to cooperate in making the list complete by sending their separates and by making corrections and additions, and especially by calling attention to meritorious articles published outside of regular journals. Reprints or correspondence should be addressed to Miss E. R. Oberly, Librarian, Bureau of Plant Industry, U. S. Dept. of Agric., Washington, D. C.

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